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Effects of free-air carbon dioxide enrichment on PAR absorption and conversion efficiency by cotton

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Abstract

Anticipated changes in global climate and atmospheric CO_2 concentrations have very important, albeit poorly understood consequences for production agriculture . Effects of these changes on plants have usually been examined in controlled-environment enclosures, glass-houses, or open-top field chambers. Beginning in 1989, an innovative experimental free-air CO_2 enrichment (FACE) facility was operated in central Arizona to evaluate crop response to increased CO_2 levels within a large, open-field production environment. Cotton (*Gossypium hirsutum* L.) was grown for three consecutive seasons under well-watered conditions and exposed to either ambient (control, about 370 μmol mol^{-1}) or elevated (FACE, 550 μmol mol^{-1}) CO_2 concentrations. Deficit irrigation regimes supplying 75% (beginning in July 1990) or 67% (beginning in mid-May 1991) of the crop's evapotranspiration requirement were included as additional treatment variables. Plant growth was monitored by periodic sampling. Canopy reflectances in visible (blue, 0.45–0.52 μm; green, 0.50–0.59 μm; red, 0.61–0.68 μm) and near-infrared (NIR; 0.79–0.89 μm) wavebands were measured frequently with an Exotech radiometer and related to absorbed photosynthetically active radiation (PAR; 0.4–0.7 μm) measured with a line quantum sensor. Dry biomass of plants in the FACE treatment was significantly ($P < 0.05$) greater than control values during each year of the study. The FACE plant canopy also absorbed significantly more PAR than controls during the early and middle portion of the 1990 and 1991 seasons. Light use efficiency (LUE, biomass produced per unit absorbed PAR) was significantly higher in FACE plots during each year. In the well-watered irrigation treatment, the 3 year mean LUE was 1.97 g MJ^{-1} for FACE and 1.56 g MJ^{-1} for controls. The deficit irrigation treatment in 1991 produced significantly smaller plants, which absorbed less PAR and had lower LUE than plants in the well-watered treatment ($P < 0.05$). No interaction was observed between CO_2 and irrigation treatments. FACE research under realistic field conditions revealed positive consequences of increased CO_2 on cotton plant

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biomass, PAR absorption, and LUE. It also demonstrated the effectiveness of this new technology for examining community-level plant responses to possible changes in global environment.

1. Introduction

Global CO_2 levels are rising steadily, as a result of human activities (Post et al., 1990). On the basis of observed trends, atmospheric concentrations may even double during the next century. The consequences of these changes for production agriculture are important because photosynthetic rates of many C_3 food and fiber crops are limited by CO_2 at present atmospheric CO_2 levels (Pearcy and Björkman, 1983). Anticipated increases in CO_2 concentrations to levels of 650 or 675 μmol mol^{-1} may boost biomass production and marketable agricultural yields by 33% provided other constraints to productivity remain non-limiting (Kimball, 1983).

Despite a large body of research evidence showing positive effects of CO_2 on plant growth (Kimball, 1983; Lawlor and Mitchell, 1991), justifiable concern has focused on the artificial environments used to conduct past experiments (Allen et al., 1992). Would results have been similar if an entire community of plants were exposed to high CO_2 levels without the artifacts induced by controlled-environment enclosures, glasshouses, or open-top chambers? This question provided impetus for developing a free-air CO_2 enrichment (FACE) facility and conducting large-scale field experiments in central Arizona using cotton as a test crop (Hendrey, 1992; Dugas and Pinter, 1994; Hendrey and Kimball, 1994).

Growth increases from relatively small CO_2-induced changes in photosynthetic efficiencies can result in large gains in season-long productivity of natural or cultivated plant populations because of the compounding effect of an ever larger light-capturing canopy. This overall increase in productivity can be separated into two components—the effective size of the canopy's light-capturing apparatus and the light use efficiency (LUE) of the canopy. The fraction of photosynthetically active radiation (PAR, 0.4–0.7 μm) absorbed by the canopy (fA_{PAR}) is a quantitative estimate of the first component. It can be measured directly with sensors above and below the canopy (Hipps et al., 1983; Gallo and Daughtry, 1986) or inferred indirectly from green leaf area index measurements, leaf angle distributions, and canopy light extinction functions (Hatfield et al., 1984; Major et al., 1991). A number of reports have demonstrated the utility of multispectral reflectance measurements for predicting fA_{PAR} of plant canopies (Kumar and Monteith, 1981; Daughtry et al., 1983; Wanjura and Hatfield, 1986; Wiegand et al., 1991; Pinter, 1993). These remote sensing approaches are rapid, efficient, and amenable to large-scale surveillance by sensors at ground, aircraft, or satellite levels. Sellers (1987), Choudhury (1987), and Baret and Guyot (1991) have addressed the functional relationships between plant productivity, leaf area index, fA_{PAR}, and canopy reflectance properties from various theoretical perspectives. Although these relationships are largely beyond the scope of this paper, it is germane to this study that reflectance-derived fA_{PAR} is a very useful and sensitive biophysical index of canopy response to growth-limiting or -enhancing changes in the environment.

The second component of gross plant productivity, LUE, is defined as the amount of biomass (g m^{-2} day^{-1}) produced per unit of absorbed photosynthetically active radiation (A_{PAR}, MJ m^{-2} day^{-1}). When growing conditions are optimum, the accumulation of plant dry matter is often proportional to the product of incident PAR and fA_{PAR} (Monteith, 1977). However, the conversion efficiencies of PAR to phytomass are sensitive to growth-limiting stresses such as temperature, water availability, nutrient status, and even atmospheric pollutants (Asrar et al., 1984; Unsworth et al., 1984; Russell et al., 1989; Demetriades-Shah et al., 1992). It is this dynamic response to environmental factors which renders LUE a useful parameter for integrating season-long conditions for growth and quantifying plant responses to experimental treatments. Quantitative estimates of fA_{PAR} and LUE are also useful for plant growth modeling (Norman and Arkebauer, 1991; Easterling et al., 1992), and for inferring photosynthetic capacity at global scales (Tucker and Sellers, 1986; Tucker et al., 1986). Within-season estimates of these biophysical parameters are anticipated to provide validation for the physiologically based COTCO2 model of cotton growth (Wall et al., 1994).

A shift from relatively small, enclosed, test environments to large-scale, open-field FACE projects also dictated that commensurate non-invasive approaches be used to evaluate whole-canopy responses to experimental treatments (Pinter et al., 1992) as opposed to the individual organ or plant responses often used in the past. With these requirements in mind, we report the use of canopy reflectance in visible and near-IR (NIR) regions of the spectrum to characterize the effects of supra-ambient atmospheric CO_2 concentrations and water stress on fA_{PAR} of cotton at daily time steps throughout the growing season. These data are then combined with daily totals of incident PAR and periodic measures of plant biomass to yield estimates of cotton LUE during three consecutive years of FACE experimentation.

2. Methods

2.1. Field site, cultural operations, and meteorological data

Observations of cotton canopy biomass, fA_{PAR}, and reflectance were made in 1989, 1990, and 1991 at the University of Arizona's Maricopa Agricultural Center (MAC) (33.07°N,111.98°W; approximately 40 km south of Phoenix, AZ; elevation 358 m). Eight circular experimental plots (about 500 m^{-2}) were located within two adjacent, 4 ha cotton fields. Soils were classified as reclaimed Trix clay loam (fine-loamy, mixed (calcareous), hyperthermic Typic Torrifluvents) (Post et al., 1988). Upland cotton (*Gossypium hirsutum* L. cv. 'Deltapine 77') was sown on raised beds in east–west rows spaced 1.02 m apart. After emergence (Table 1), plants were thinned to a population of about 10 plants m^{-2}. Cultural practices (cultivation, insect control, soil nutrient levels, etc.) were typical of those recommended by state extension service and university research staff. Experiments were terminated and final harvests taken in

Table 1
Sowing, emergence and harvest dates (DOY refers to day of year), seasonal meteorological parameters and irrigation amounts for 3 years of FACE experiments with cotton at the Maricopa Agricultural Center

	1989	1990	1991
Sowing	17 April (DOY 107)	23 April (DOY 113)	16 April (DOY 106)
Emergence	28 April (DOY 118)	2 May (DOY 122)	25 April (DOY 115)
Harvest	17 September (DOY 260)	17 September (DOY 260)	16 September (DOY 259)
Cumulative incident radiation ($MJ\,m^{-2}$; PAR)	1803	1716	1820
Mean daily temperature maximum (°C) (range; SD)	38.3 (23.2–45.8; 3.9)	37.6 (23.5–49.4; 4.4)	36.5 (23.6–43.6; 4.2)
Mean daily temperature minimum (°C) (range; SD)	19.2 (7.2–27.3; 4.5)	19.7 (9.3–28.9; 4.3)	18.1 (6.3–26.7; 4.9)
Mean daily temperature mean (°C) (range; SD)	28.7 (17.6–35.1; 3.7)	28.4 (18.1–37.0; 3.5)	27.2 (16.1–32.2; 3.9)
Cumulative heat units (°C days)[a]	1914	1911	1857
Mean daily VPD (kPa) (range; SD)	3.04 (0.60–4.70; 0.82)	2.77 (0.20–5.90; 1.12)	3.19 (0.80–4.60; 0.82)
Cumulative potential evapotranspiration (mm)[b]	1215	1125	1242
Seasonal precipitation (mm)[c]	22	125	41
Seasonal irrigation amounts (mm)			
Wet treatment	1270	1190	1048
Dry treatment	NA	1060	792
Ratio (water applied/PET)			
Wet treatment	1.06	1.17	0.88
Dry treatment	NA	1.05	0.65

[a] Computed from hourly AZMET temperatures with a base temperature of 12.8°C and an upper temperature threshold of 30°C for cotton (Appendix G of Brown, 1989).
[b] Reference potential evapotranspiration was computed from hourly AZMET weather data using the modified Penman equation (Appendix G of Brown, 1989).
[c] Rainfall for 1989 was taken from AZMET records; 1990 and 1991 data were obtained in the field.
NA, Not applicable.

mid-September. Additional details on experimental protocol and cultural practices have been given by Mauney et al. (1992, 1994). Summary weather data from the Maricopa Station of the Arizona Meteorological Network (AZMET; Brown, 1989) are given in Table 1. This station was approximately 2 km from the experimental field.

2.2. Experimental treatments

Carbon dioxide levels

Cotton plants were exposed to enriched (FACE, about 550 μmol mol^{-1}) and ambient (control, about 370 μmol mol^{-1}) CO_2 levels; treatments were replicated four times. In the FACE treatment plots, CO_2 enrichment began shortly after emergence and continued during daylight hours until plants were harvested. CO_2

concentrations were maintained by injection of CO_2-enriched air from manifolds (of 23–27 m diameter) surrounding experimental plots. CO_2 concentrations were monitored via a sampling port about 150 mm above the plant canopy in the center of each plot. Combined with wind speed and direction, these concentrations formed the basis for feedback control of CO_2 injection from vertical risers on the manifold. FACE and control plots were exposed to similar ambient CO_2 concentrations at night (often more than 400 μmol mol^{-1} (Nagy et al., 1994)). In 1990 and 1991, control plots were encircled with manifolds similar to those around the FACE plots, but without the mechanisms required to inject gas into the canopy. Controls were located a minimum of 90 m from FACE plots, and received negligible CO_2 input from treated sites (Nagy et al., 1994). Plot and field diagrams, the FACE apparatus, CO_2 control strategies, and overall system performance have been discussed in detail by Lewin et al. (1994), Mauney et al. (1994), and Nagy et al. (1994).

Irrigation levels

The soil was irrigated using micro-irrigation (drip) tubing that was buried at 0.18–0.25 m depth. In 1989, all plots were well watered ('wet' treatment); irrigation was based on full-season consumptive use requirements of cotton as determined from estimates of potential evapotranspiration (PET) obtained from AZMET. In subsequent years, wet treatments received irrigation amounts equivalent to that evaporated from a class A pan (1990) and PET based on AZMET (1991). In 1990 and 1991, CO_2 treatment plots were split to test the effect of deficit irrigation ('dry' treatment) on cotton response to CO_2. Dry plots were irrigated on the same days as wet plots, but received only 75% and 67% of the water supplied to the wet plots during 1990 and 1991, respectively. This differential irrigation scheme was initiated on 3 July in 1990 (day of year (DOY) 184) and on 20 May in 1991 (DOY 140). The combined amounts of irrigation and rainfall from planting to harvest averaged 1232 mm across all years for the wet treatment, whereas dry treatments received 1185 mm in 1990 and considerably less (833 mm) in 1991 (Table 1; Hunsaker et al., 1994; Mauney et al., 1994).

2.3. Experimental measurements

Plant growth and carbon content

Biomass was measured by destructive plant sampling at 1–2 week intervals during the growing season. There were eight such harvests in 1989, 15 in 1990, and 17 in 1991. The sampling approach consisted of pulling every third cotton plant (with as much of the lateral root and taproot structures as possible) from three separate segments of plant row of 1 m length in all replicates of each CO_2 and irrigation treatment. This was equivalent to sampling all the plants in a contiguous 1.02 m^2 area, but did not leave completely bare spots which might have adversely affected the response of remaining plants or the aerodynamics of CO_2 flow. Dried biomass was measured separately for root, stem, leaf, and fruiting structures.

Percentage carbon (C) contents of cotton root, stem, and leaf tissues were measured in 1990 (G. Huluka, personal communication, 1991) and used to compute LUE on a molar basis. For control plants, roots were 40.7% C, shoots were 44.3% C, and leaves were 39.0% C. Results were similar for FACE plants (roots 41.8% C, shoots 44.4% C, and leaves 39.6% C). Carbon content of cotton bolls was estimated to be 54.0% for both FACE and control plants (J. Amthor, personal communication, 1991). This estimate is based on a 33% lint (at 40% C) and 67% seed (at 62% C) composition of bolls.

PAR absorption

Canopy light absorptance in PAR wavelengths (fA_{PAR}) was estimated from observations of incident (I_{PAR}), transmitted (T_{PAR}), and reflected (R_{PAR}) components of the radiation balance measured in μmol m^{-2} s^{-1}. These were obtained on three dates in 1990 and seven in 1991 using a single, hand-held, line quantum sensor (LI-191; Li-Cor, Lincoln, NE, USA) for all treatments and replicates. Data were recorded on a Polycorder (Model 516B; Omnidata International, Logan, UT), and were completed within a 3 h interval centered on solar noon. Observations were conducted under mostly clear-sky conditions with no cloud interference with the direct beam solar radiation.

Measurements were made along a transect that spanned six adjacent plant rows in the final harvest area of the experimental plot space (Mauney et al., 1994). The sequence began with six measurements of I_{PAR} with the line quantum sensor horizontal and viewing straight up. Next, T_{PAR} was obtained by inserting the sensor (of 1 m length) beneath the canopy at the level of the soil bed and perpendicular to the row orientation. Measurements were repeated for each row along the transect. Finally, R_{PAR} was determined over the same six rows using an inverted sensor (again perpendicular to the rows) about 0.50–0.75 m above the canopy. Similar measurements were made at a separate 3 m × 8 m bare soil plot in the same field. The entire sequence of measurements required 3–4 min per plot. A light balance equation (Gallo and Daughtry, 1986) was then used to compute the canopy fA_{PAR}:

$$fA_{PAR} = 1.0 - (T_{PAR}/I_{PAR}) - (R_{PAR}/I_{PAR}) + fR_{PARs} \tag{1}$$

where the fraction of PAR reflected from the soil beneath the canopy (fR_{PARs}) was estimated as the product of fractional canopy transmittance (T_{PAR}/I_{PAR}) and the PAR reflectance from the bare soil plot (R_{PARs}/I_{PAR}).

Reflectance and vegetation indices

Canopy and soil reflectance factors were measured two to four times a week during the growing season, depending on weather conditions and rates of plant growth. In 1989, 40 data sets were acquired from 17 May to 20 September. This was expanded to 44 data sets in 1990 (30 April–18 September) and 70 in 1991 (19 April–15 September). Observations were made using a hand-held radiometer (Model 100BX; Exotech, Gaithersburg, MD) equipped with 15° field-of-view optics and spectral bandpass filters spanning three visible (blue, 0.45–0.52 μm; green, 0.50–0.59 μm; red, 0.61–0.68 μm) and one NIR (0.79–0.89 μm) wavelength intervals. In all years, the radiometer was deployed in a bare soil target and along a permanent north–south transect in the undisturbed final harvest area of each subplot. In 1989, the transect crossed 12 cotton rows in four replicates of FACE and control treatments. In 1990 and 1991, the transect length was reduced to a six-row segment of the canopy, because the CO_2 treatments were split to accommodate wet and dry irrigation treatments.

The radiometer was extended at arm's length towards the east, held approximately 1.5 m above the soil surface and deployed in a nadir orientation. Thus each lens viewed an area that was approximately 0.26 m in diameter when the cotton plants were 0.5 m in height. Data were collected at a rate of four evenly spaced measurements per row of plants, yielding 48 individual measurements per wavelength interval per plot in 1989, and 24 in subsequent years. The entire measurement sequence over all experimental treatments and replicates required approximately 25–35 min to complete.

Multispectral observations were centered on a morning time period corresponding to a solar zenith angle (Θ_S) of 45° to minimize the effects of changing illumination angles on directional canopy reflectance as the season progressed (Pinter et al., 1990). The mean solar azimuth during measurements was 100°; the range was from 87° in June to 134° in September. Qualitative observations of weather, sky conditions, and canopy appearance were recorded at time of data collection. In the analyses which follow, all multispectral data were used regardless of sky conditions.

Analog signals from the radiometer were recorded on a portable data acquisition system (Polycorder; Omnidata International), which also registered the time when measurements were taken. Single band reflectance factors were calculated as the ratio of radiant excitance measured over each cotton target to irradiance inferred from a time-based linear interpolation of data collected at approximately 15 min intervals over a horizontally positioned, 0.6 m × 0.6 m, painted $BaSO_4$ reference panel. Correction factors were applied to the $BaSO_4$ data to compensate for its non-Lambertian reflectance characteristics. The normalized difference vegetation index (NDVI) was computed as the difference of NIR and red reflectances divided by their sum:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{Red})/(\mathrm{NIR} + \mathrm{Red})$$

Daily NDVI values were estimated with a sliding third-order polynomial curve-fitting technique.

2.4. Light use efficiency

Several workers have suggested that the traditional method for equating LUE to the slope of the cumulative phytomass vs cumulative A_{PAR} function is inappropriate from a statistical point of view because sequential values of these parameters during the season are not independent of one another (Russell et al., 1989; Demetriades-Shah et al., 1992). One solution to that concern, and the approach we pursued in this study, was to compute LUE for discrete intervals during the season. On a mass equivalent basis, the numerator for LUE becomes the difference in biomass from one sampling interval to the next; the denominator becomes the difference in cumulative A_{PAR} on each date:

$$\mathrm{LUE} = \delta DM/\delta A_{\mathrm{PAR}} = (DM_2 - DM_1)/(\textstyle\sum A_{\mathrm{PAR}_2} - \sum A_{\mathrm{PAR}_1}) \quad (2)$$

where DM is total dry biomass (g m^{-2}), $\sum A_{\mathrm{PAR}}$ is the cumulative daily product of photosynthetic irradiance (PI, $\mathrm{MJ_{PAR}}$ m^{-2}) and fA_{PAR} estimated from canopy reflectance measurements, and numerical subscripts refer to separate sampling dates. Total biomass values were first smoothed with a two-term running average. Photosynthetic irradiance was approximated as 0.45 times incident global solar radiation (ISR, in MJ; Meek et al. (1984)) measured at the AZMET meteorological station. Computation of LUE on a molar basis (mol C mol^{-1} photon A_{PAR}) required that (1) total DM on each date be converted to the carbon equivalent of its component parts (i.e. roots, stems, leaves, and fruit) using the fraction carbon given above, and (2) $\sum A_{PAR}$ of Eq. (2) be expressed in photon flux density units according to the following relationship:

$$PI = 1.83 \times \text{ISR}$$

which was determined independently through least-squares regression of hourly PAR values from a Li-Cor quantum sensor and hourly ISR from the AZMET station, and compares favorably with a conversion coefficient of 1.91 mol photons MJ^{-1} ISR reported for a clear day in Phoenix (Meek et al., 1984).

2.5. Statistical analysis

Data were analyzed using the statistical procedures of the Statistical Analysis Systems Institute Inc. (SAS Institute Inc., 1985). In 1989, the CO_2 treatment effect was tested with the residual mean square (error) in the analysis. In 1990 and 1991, the same ANOVA model was used until differential irrigations were initiated (DOY 184 in 1990; DOY 140 in 1991). Thereafter, a split-plot ANOVA model was used which included CO_2, replication, irrigation, and the interaction terms. The CO_2 treatment effect (main plot) was tested using the mean square of the CO_2 by replicate interaction as the error term. Irrigation (subplot) and CO_2 by irrigation were tested using the mean square of the CO_2 by irrigation by replicate interaction as the error term, provided this interaction was significant at $P < 0.20$. If the interaction was not significant, it was removed from the model and the residual mean square (error) was used to test significance of treatment means. Differences were considered significant if the probability (P) of obtaining a larger F statistic was less than 0.05.

3. Results

3.1. Plant biomass

Cotton plant growth, phenology (Mauney et al., 1992, 1994), and pest problems (D.H. Akey, personal communication, 1991) in our experiments were typical of those observed in commercial fields in central Arizona during the same period. The control wet irrigation treatment produced yields of seed and lint that were higher than county averages in all 3 years (Mauney et al., 1992, 1994). Figure 1 shows average total dry biomass that was estimated from periodic destructive samples of cotton populations in each treatment. It reveals relatively slow growth of young plants during April and

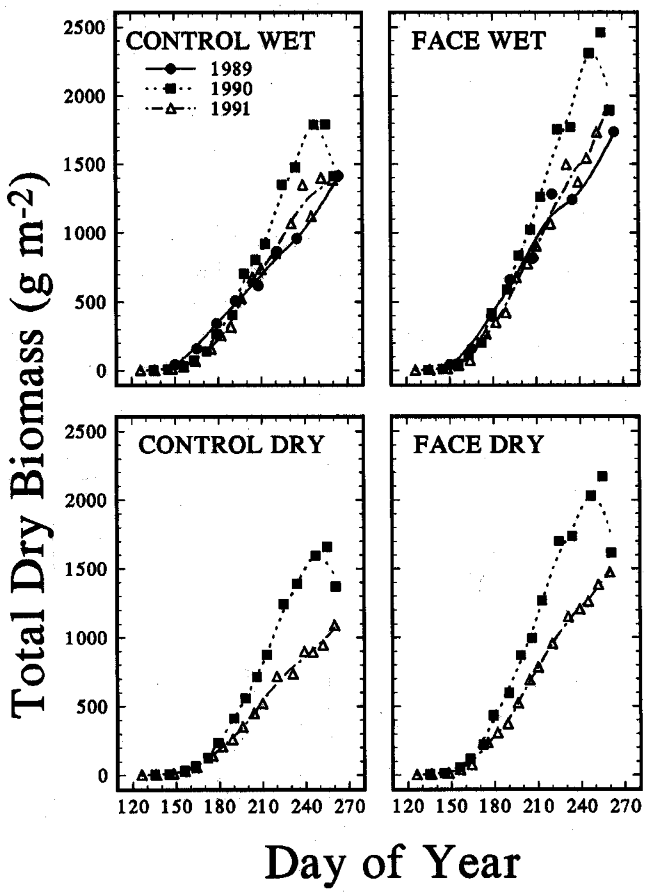

Fig. 1. Total dry biomass (g m^{-2}) of cotton plants determined by periodic destructive sampling techniques. A single data point represents an average of four replicates in each CO_2 and irrigation treatment combination. Trend curves were generated by a locally weighted, least-squares regression smoothing technique.

May of each year. Then, beginning in June (DOY 152) and coincident with early square development, rates of biomass accumulation increased exponentially, and remained moderately high until final harvest in mid-September.

Plant growth was related to experimental CO_2 treatments, water management and weather. During each year of the experiment, trends were similar; highest total biomass was found in the FACE wet treatments, and lowest levels were observed in the control dry treatment (1990 and 1991). Higher rainfall and larger irrigation amounts caused much higher biomass in the wet treatment in 1990 than in either 1989 or 1991. Notable biomass differences also appeared between years in control dry and FACE dry treatments, reflecting the earlier implementation and greater soil water deficit of the dry irrigation regime of 1991. A change in sampling and processing technique for the last sample of the 1990 season was believed responsible for the abrupt and otherwise unexplained decline in biomass across all treatments on that date (J. Mauney, personal communication, 1991). As a result, those specific data were excluded from the light use efficiency computations reported below.

Effects of experimental treatments on total biomass were examined by normalizing average data from FACE subplots with respect to the controls in the same irrigation treatment (i.e. ratios of FACE to control; upper half of Fig. 2). The variation we observed in these ratios from one date to the next was large. Nevertheless, these data show a consistent pattern of increased biomass production associated with elevated CO_2 levels. ANOVA revealed significant differences in total dry biomass between C control and FACE treatments for three of eight sampling dates in 1989. In the second and third years of the experiment, significant differences between control and FACE occurred on all but three of the sampling dates. When averaged over the entire season, we found that elevated CO_2 increased biomass by $22 \pm 5.8\%$ (1 SE) in 1989, $37 \pm 3.3\%$ in 1990, and $28 \pm 3.6\%$ in 1991 for the non-limiting soil moisture

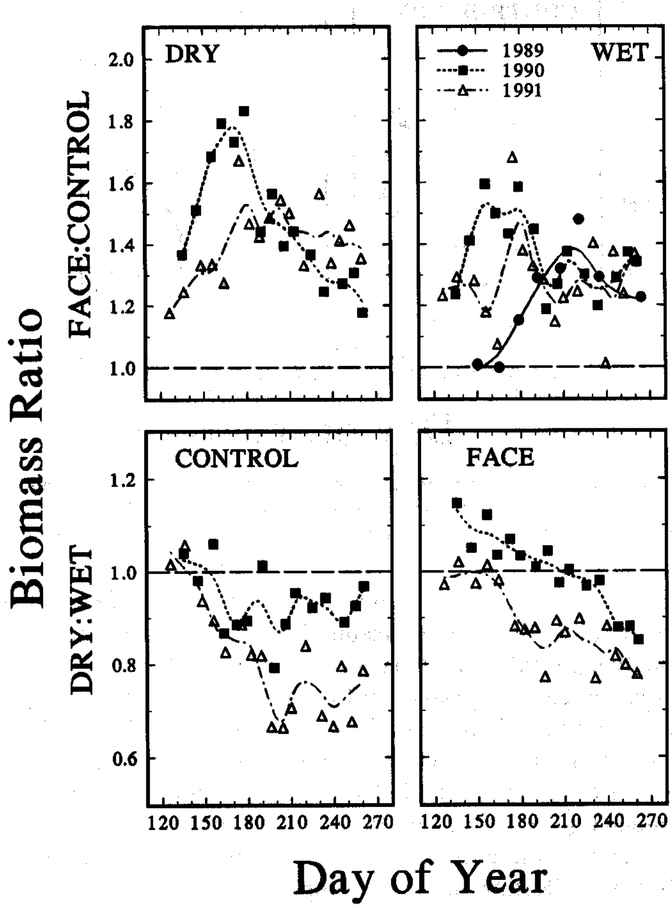

Fig. 2. Ratios computed as total dry biomass in the FACE treatments divided by their counterpart control values, and total dry biomass in the dry treatments divided by counterpart values for the wet treatments. Data points and trend curves follow the same convention as in Fig. 1.

conditions of the wet treatment. Biomass increases associated with elevated CO_2 were similar for the dry treatment plots in 1990 (+36 ± 4.0%) and considerably higher (+43 ± 2.8%) in 1991.

Comparisons between dry and wet irrigation regimes within each CO_2 level were likewise facilitated by computing biomass ratios and plotting them against sampling date (lower half of Fig. 2). Although plants in the FACE dry treatment appear slightly larger than their wet counterparts early in 1990, this occurred before any differential treatments had started and the difference was not statistically significant. Several weeks after the deficit irrigation regime was begun we observed a gradual decline in the dry:wet biomass ratio. After 3 July 1990 (DOY 184), plants in the dry treatment averaged 5 ± 2.3% (1 SE) and 8 ± 2.1% lower biomass than their wet analogs in FACE and control plots, respectively. However, ANOVA revealed that the dry irrigation treatment did not produce a significantly smaller plant until the last sampling date. In 1991, effects of the dry irrigation treatment were more substantial. When averaged for sampling dates after the dry treatment had been started (later than DOY 120), plants in the FACE dry treatment were 13 ± 2.0% smaller than the counterpart FACE wet plants, and those in the control dry treatment were 22 ± 2.4% smaller than in the control wet treatment. In 1991, the earlier initiation and more severe water stress imposed by the dry treatment caused a significant irrigation effect on 10 out of 17 sampling dates. Further analysis of biomass data revealed that the interaction term (CO_2 by irrigation) was not significant on any sampling date in 1990 or 1991.

3.2. CO_2 and irrigation effects on fA_{PAR}

Measurements with the line quantum sensor

Rapid plant growth and expansion of cotton leaves during early summer increased canopy cover and produced corresponding increases in measured fA_{PAR} in each CO_2 and irrigation treatment (Fig. 3). Although the 1990 data set was limited, it suggested a vigorous doubling of fA_{PAR} during a 3 week period in late June and early July. A more complete set of observations in the following year revealed fA_{PAR} values lagging those of 1990 by about 1 week. The fA_{PAR} values of FACE plots were consistently higher than those of controls until the end of July in both years. ANOVA showed that the CO_2 treatment means for fA_{PAR} were significantly different on one date (DOY 171) in 1990 and three (DOY 183–212) in 1991.

Irrigation had a more pronounced effect on the measured fA_{PAR} than did CO_2 treatment. Plants in the wet treatment were generally larger and capable of absorbing more PAR than those in the dry treatment. Differences developed late in the 1990 season, because the differential irrigations were not begun until 3 July and substantial amounts of rain fell shortly thereafter. Nevertheless, a highly significant difference in fA_{PAR} was found between irrigation treatment means by late August in 1990 (DOY 241). Irrigation had a significant effect on fA_{PAR} on each measurement date in 1991. During 1991, fA_{PAR} attained maximum values of 0.90–0.95 by the end of July (DOY 212) in the wet treatments and remained at those levels until harvest 6 weeks later. By contrast, fA_{PAR} of dry treatments increased systematically at every

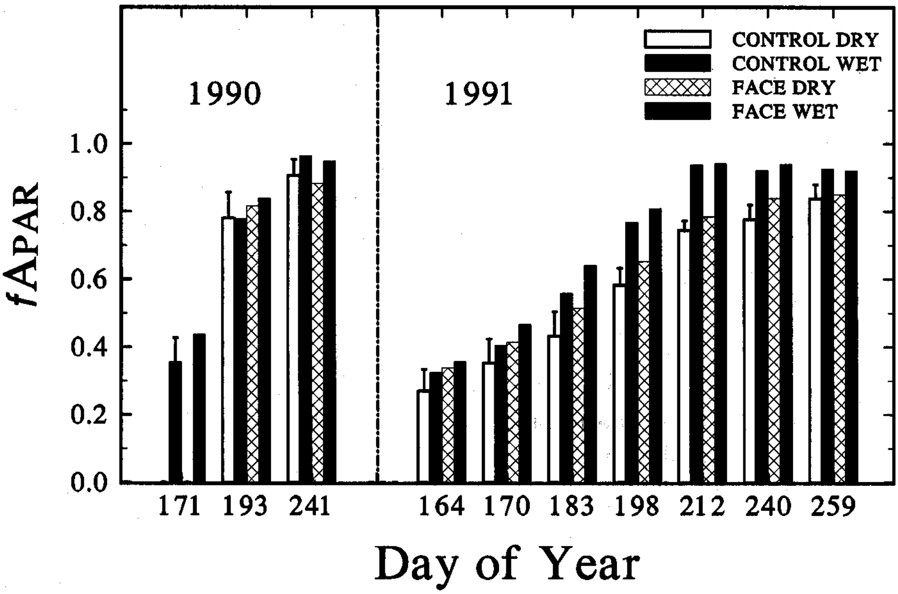

Fig. 3. Fraction of absorbed photosynthetically active radiation (fA_{PAR}) measured using a line quantum sensor in cotton during the 1990 and 1991 experiments. Error bars show the appropriate least significant difference (LSD; $P < 0.05$) for testing differences between any treatment combination within a given day.

measurement date in 1991. At the end of the season, the canopy's light-capturing apparatus in the dry treatments were nearly as great as that in wet treatments despite large absolute differences during July and August. The interaction between CO_2 and irrigation treatments was not statistically significant ($P < 0.05$) on any of the measurement dates.

3.3. Relationship between fA_{PAR} and NDVI

A major goal in our research was to develop a relationship for estimating season trends in fA_{PAR} from NDVI because of the ease with which the latter parameter could be measured by non-invasive means. Figure 4 reveals that midday line quantum sensor measurements of fA_{PAR} were very highly correlated with NDVI measured on the same dates at a morning Θ_{S} of 45°. An important finding was that the relationship was independent of CO_2 and irrigation treatments and very similar across years. As measured fA_{PAR} data were not obtained until cotton plants had already covered 25–35% of the ground (mid-June), fA_{PAR} and NDVI measured over the bare soil target were also included in the regression. This anchored the quadratic function at values expected for a cotton field before emergence and increased the predictive value of the resulting relationship for fA_{PAR} estimates below 25%.

Frequent NDVI values facilitated the prediction of fA_{PAR} early in the season, and also in 1989 when line quantum sensor observations were not made (Fig. 5). Results illustrated that fA_{PAR} increased most rapidly during the middle portion of the

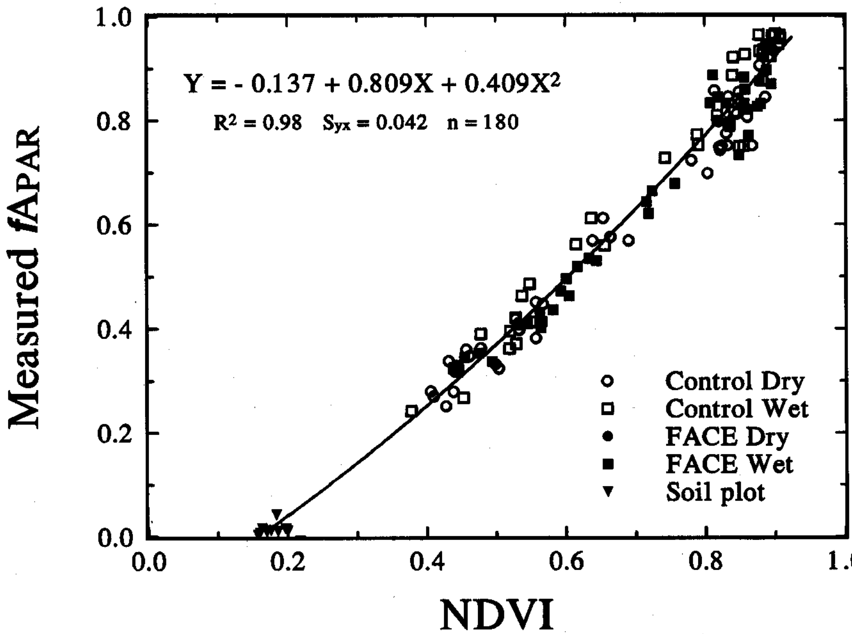

Fig. 4. Midday fraction of absorbed photosynthetically active radiation (fA_{PAR}) measured with a line quantum sensor vs the normalized difference vegetation index (NDVI) over the Trix clay loam soil and cotton in CO_2 and irrigation treatments in 1990 and 1991.

growing season and then, provided conditions were favorable, asymptotically approached maximum values of 0.90–0.95 units. There was considerable variation between years within a given experimental treatment. In 1989, for example, cotton in FACE wet and control wet treatments had higher fA_{PAR} from late May to mid-June (DOY 140–170) than for the same period in subsequent years, perhaps owing to more favorable early season growing conditions. Midway in the 1989 season, however, fA_{PAR} in the wet treatments dropped far below those of 1990 and 1991. Partially clogged subsurface drip irrigation tubing (Mauney et al., 1992) and infestation by herbivorous spider mites (D.H. Akey, personal communication, 1991) were responsible for the decline in 1989. An inflection point in the trend lines for fA_{PAR} after DOY 170 (1991) alerted experiment managers to unintentional plant water stress that was developing in the wet treatment. After increasing the frequency and amount of irrigations, the water stress was relieved and fA_{PAR} resumed its increase. The differences between dry treatments from late June (DOY 170) to the end of the season suggest that the deficit irrigation regime limited light absorption to a much greater extent in 1991 than in 1990, a conclusion that was also confirmed by biomass data presented above.

The effects of experimental treatments on light absorption by the canopy are underscored by fA_{PAR} ratios of Fig. 6. In 1989, the CO_2 apparatus was not turned on until almost 1 month after the plants had emerged. Although the FACE treatment displayed a 5–10% fA_{PAR} advantage over controls during June and early July of that

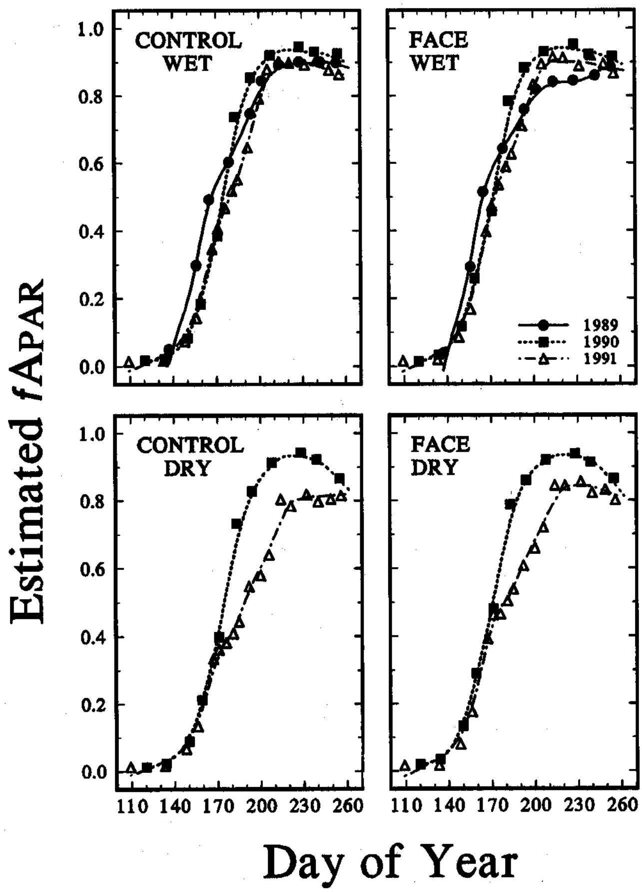

Fig. 5. Estimated fraction of absorbed photosynthetically active radiation (fA_{PAR}) estimated using the normalized difference vegetation index (NDVI) for each treatment combination during 1989, 1990, and 1991. For clarity, fA_{PAR} trends are emphasized by smoothed lines computed using a locally weighted polynomial regression technique for all days (including cloudy dates) that data were collected, although only every fourth datum is shown.

year (DOY 155–190), the difference was not statistically significant. In the following years, however, CO_2 enrichment was begun at emergence, and statistically higher fA_{PAR} values were found in FACE treatment from mid-May until late June in 1990 and from mid-June until mid-August in 1991. FACE canopies attained 100% ground cover earlier than controls, but the latter treatment eventually caught up and fA_{PAR} ratios converged to unity. In 1989, problems with the irrigation system and spider mite infestations were more severe in the FACE treatment than in controls. The result was significantly lower fA_{PAR} in FACE in early August 1989 (DOY 221) compared with subsequent years. Our data also showed that cotton in the FACE dry treatment (1991) maintained a considerable fA_{PAR} advantage over plants in the control dry treatment until the end of the season. The fA_{PAR} ratios between dry and wet

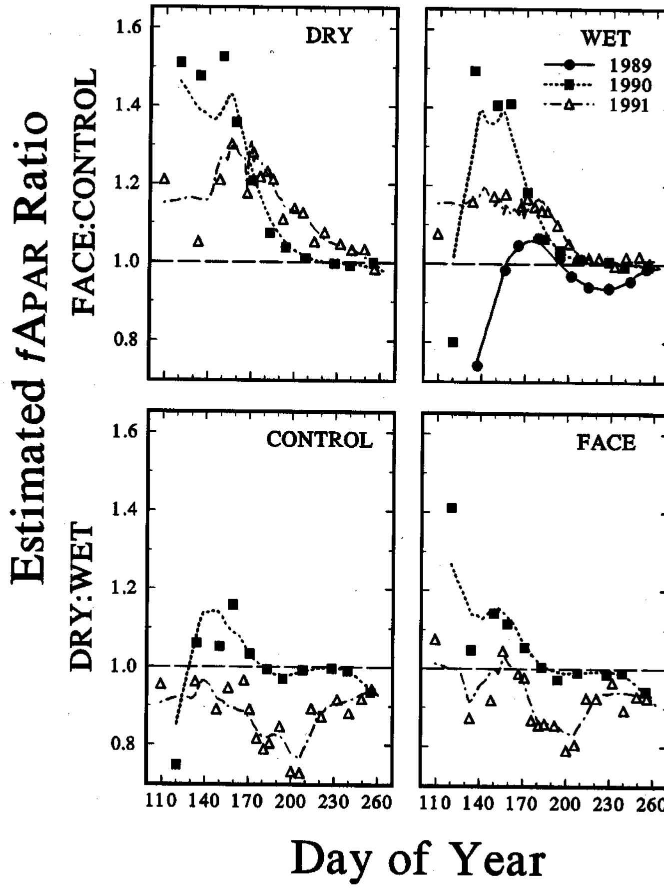

Fig. 6. Ratios computed as NDVI-estimated fA_{PAR} in the FACE treatments divided by their counterpart control values, and NDVI-estimated fA_{PAR} in the dry treatments divided by counterpart values for the wet treatments. Data points and trend curves follow the same convention as in Fig 5.

irrigation treatments (lower half of Fig. 6) mirror the effects on biomass discussed above. ANOVA revealed that fA_{PAR} of the dry treatment was significantly lower than that of the wet treatment from early September (DOY 247) until harvest in 1990 and from late June (DOY 175) until harvest in 1991.

3.4. Light use efficiency

Light use efficiencies were computed independently for each biomass sampling interval and then averaged by CO_2 and irrigation treatment for the entire season (Table 2). The 3 year mean LUE for cotton exposed to ambient CO_2 levels in our study was 1.51 g MJ^{-1}. This value compares favorably with the 1.24–1.66 g MJ^{-1} range of efficiencies reported for several cultivars of cotton grown in Texas (Rosenthal and Gerik, 1991), but is substantially lower than the 2.55 g MJ^{-1}

Table 2
Light use efficiency (LUE) treatment means for cotton grown at MAC from 1989 to 1991

(A) Mass basis

Year	CO_2 Treatment means					Irrigation treatment means				
	Control LUE ($g\,MJ^{-1}$)	n	FACE LUE ($g\,MJ^{-1}$)	n	Probability level	Dry LUE ($g\,MJ^{-1}$)	n	Wet LUE ($g\,MJ^{-1}$)	n	Probability level
1989	1.37	24	1.83	24	0.011	–	–	1.60	48	–
1990	1.73	104	2.10	94	0.007	1.80	99	2.01	99	0.085 NS
1991	1.42	120	1.75	120	0.016	1.50	120	1.67	120	0.007
3 year averages	1.51		1.89			1.65		1.76		

(B) Molar basis

Year	Control LUE ($\mu mol\,mol^{-1}$)	n	FACE LUE ($\mu mol\,mol^{-1}$)	n	Probability level	Dry LUE ($\mu mol\,mol^{-1}$)	n	Wet LUE ($\mu mol\,mol^{-1}$)	n	Probability level
1989	13.07	24	17.61	24	0.011	–	–	15.33	48	–
1990	15.94	104	19.67	94	0.005	16.81	99	18.60	99	0.102 NS
1991	13.34	120	16.93	120	0.008	14.32	120	15.95	120	0.008
3 year averages	14.12		18.07			15.56		16.63		

LUE obtained from time periods that were directly affected by lightning-interrupted CO_2 deliverly to FACE during part of July 1990 (Lewin et al., 1994) were excluded from the analysis. Sample size (n) is number of individual LUE estimates included in overall mean. Probability level is the probability of obtaining a more significant F statistic based on chance alone.

reported by Howell and Musick (1985) for irrigated conditions of central California.

We observed considerable variation in LUE depending on year and treatment. Highest LUE occurred during 1990, a season that was not unusual in terms of heat unit accumulations or average daily temperatures (Table 1) but was punctuated by two atypical hot periods which occurred during flowering in June. In fact, maximum daily temperatures exceeded 44°C on 12 dates (including a record hourly mean air temperature of 49.4°C) during 1990, compared with only one date in 1989 and none in 1991. These high temperatures may have reduced fruit retention (Reddy et al., 1992) and lint yield (Mauney et al., 1994), and stimulated more vegetative biomass production in 1990. Despite the high temperatures, we did observe lower average vapor pressure deficits (VPD) in 1990 compared with preceding and following years (Table 1), and LUE has been inversely correlated with VPD for several crops (Stockle and Kiniry, 1990). However, we believe a more mechanistic explanation for higher LUE in 1990 rests with relatively low potential evapotranspiration (PET), which was coupled with high irrigation and ample rainfall to produce more favorable conditions for growth in 1990. Table 1 shows that 16% more water was applied to the wet irrigation treatment than required by the AZMET estimate of reference PET. Seasonal evapotranspiration data of Hunsaker et al. (1994) also reveal that the cotton crop used more water in 1990 than 1991.

Experimental treatment effects on LUE were tested separately for each year of the experiment using ANOVA. LUE for cotton in the FACE treatment was significantly higher than in controls during each year. Atmospheric enrichment to 550 μmol mol^{-1} CO_2 resulted in a 3 year mean LUE of 1.89 g MJ^{-1}, a 25% increase over control values. The effect of irrigation on LUE was not significant in 1990, a result influenced by the late initiation of the dry treatment and relatively small differences in the actual amount of water applied (Table 1) compared with the wet treatment. In 1991, the irrigation effect on LUE was highly significant, with cotton in the dry treatment averaging 10% lower LUE than the wet. No interaction was detected between CO_2 and irrigation treatments in either 1990 or 1991.

LUE was also averaged separately for the various CO_2 and irrigation treatment combinations (Fig. 7). Observed trends were identical during each year of the study; the cotton in the FACE wet treatment displayed the highest LUE, followed by plants in the FACE dry, control wet, and control dry treatments, in that order. In the second and third years of the study, the FACE treatment produced a similar 20–23% increase in LUE compared with controls regardless of whether cotton was subjected to the wet or dry irrigation treatment, suggesting that a rise in atmospheric CO_2 concentrations may partially compensate for plant stress caused by water shortages.

When expressed on a micromole C per mole photon A_{PAR} basis, LUE takes into account the bioenergetic costs of producing vegetative vs reproductive tissues. In molar units (Table 2 and Fig. 8), the increase in LUE of the FACE treatments over the controls was slightly larger (28%) than when computed on an energy basis, owing to proportionately higher carbon content and biomass of fruiting structures in CO_2-enriched plants (Mauney et al., 1994).

Because LUE includes a term related to plant cover (fA_{PAR}) in its denominator, it is

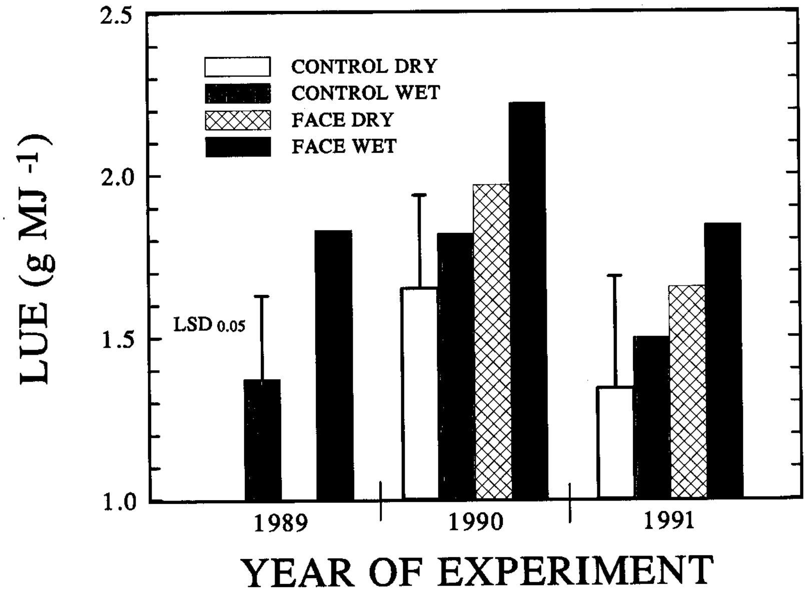

Fig. 7. Light use efficiency (LUE) on a mass basis (g MJ^{-1} A_{PAR}) for separate CO_2 and irrigation treatment combinations during 1989, 1990, and 1991. Error bars show the appropriate least significant difference (LSD; $P < 0.05$) for testing differences between any treatment combination within a given year.

largely independent of leaf area index. This unique property of LUE makes it a more powerful and valid parameter for comparing population responses to CO_2 and water treatment variables than simple changes in plant biomass per unit time. However, there are several important caveats concerning oversimplified interpretations of plant growth as a function of PAR absorbed by the canopy which deserve further mention here. From a biological perspective, LUE ignores system losses related to plant respiration, senescence, and abscission of organs, and losses caused by disease, herbivory, and sampling inefficiency. Our estimates of LUE will be affected to the extent that these unaccounted losses may differ between experimental treatments. In addition, we make the assumption that daily A_{PAR} totals can be approximated from midday fA_{PAR} multiplied by daily PI totals. As midday fA_{PAR} estimates will tend to underestimate true fA_{PAR} at large Θ_S, our daily A_{PAR} would also be lower. However, considering the diurnal distribution of PI, and empirical data showing fA_{PAR} for cotton rows oriented east–west to be relatively uniform over most of the day (Richardson and Wiegand, 1988), we believe this problem to be of relatively minor importance.

4. Summary and implications

The FACE research facility provided a unique opportunity to study the effects of increased CO_2 on cotton plant performance under natural field conditions and at

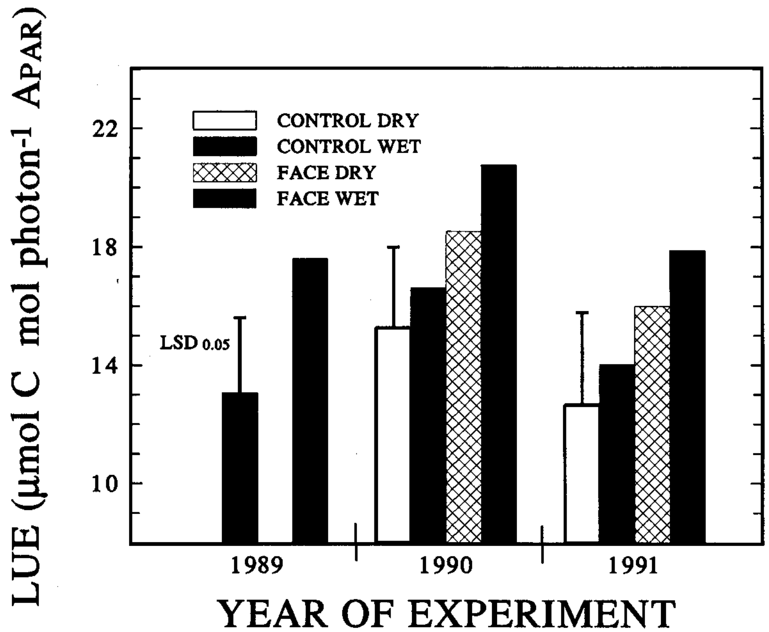

Fig. 8. Light use efficiency (LUE) on a molar basis (μmol C per mol photon A_{PAR}) for separate CO_2 and irrigation treatment combinations during 1989, 1990, and 1991. Error bars show the appropriate least significant difference (LSD; $P < 0.05$) for testing differences between any treatment combination within a given year.

spatial scales comparable with those of a commercially grown crop. Our results on cotton plant growth were consistent with those reported in the past for open-top chambers and greenhouses (Kimball and Mauney, 1993). During the 3 years of this study, cotton plants grown under well-watered conditions at FACE CO_2 concentrations of 550 μmol mol^{-1} averaged 29% more biomass than control plants at ambient CO_2 concentrations (about 370 μmol mol^{-1}). When supplied with approximately 67% of seasonal consumptive water requirements (1991), cotton plants in the FACE treatment produced 40% greater biomass than their counterpart controls.

Research in the FACE facility also revealed several important effects of higher CO_2 concentrations that could not have been tested satisfactorily at the plant community level using the currently available artificially enclosed chambers. We found, for example, that in 2 out of 3 years, cotton grown in supra-ambient CO_2 treatments had 15–40% higher light absorption in PAR wavelengths during the first half of the growing season. This is a very important factor affecting potential yield in an indeterminate fruiting crop such as cotton. We also observed an average 25% increase in light use efficiency of cotton in the FACE treatment.

Overall, our results suggest that projected increases in atmospheric CO_2 will have a positive effect on cotton production. This effect appears to be independent of moderate levels of plant water stress. Our findings emphasize the potential usefulness of similar techniques by researchers for monitoring long-term plant responses to possible changes in climate. They also provide a strong rationale for continuing research on other agricultural and natural plant communities using the FACE facility.

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